ECOLOGICAL COMPETITION AMONG THREE AND FOUR SPECIES

Leopoldo MILLAN; José L. SALES; Ricardo H. VELASCO- and
Ezio MARCHI.
Instituto de Matemática Aplicada San Luis
Universidad Nacional de San Luis
Consejo Nacional de Investigaciones Científicas y Técnicas
Argentina.

Abstract. In the present paper we study the competitive aspect among three and four species based on Volterra's equations for particular cases. Even though each case is particular, all such cases are still quite general. The main results of the paper is the deduction of the existence of the cycle in the three and four species studies. The period and madium values are studied. Some interesting examples are also considered and different graphics are shown.

Keywords. Theoretical Ecology- The Lotka -Volterra Model- Ecosystem Model- Population Dynamics

1.INTRODUCTION

The analysis for two competitive species done by Volterra is well known. Volterra's main conclusion is about the existence of the cycle between the population of two species which are usually considered as prey predator. In another case when the two species are in open competition for the same resource no cycle appears.

However, this analysis for more than two species is based on strong assumptions about the coefficients that define the equations of the interaction of the species. Therefore the obtained results and conclusions are somewhat weak and only apply in very special cases.

In the present paper we will describe the competition among three and four species following the overall scheme given by Volterra (1). The three species under considerarion, in the first place are two preies which have no interaction between each other and a predator. We derived the existence of a cycle among the three species in such a way that both preies follow the same phase. The computation of the period is presented and some studies about the medium number of individuals are considered. Interesting curves are also shown. Secondly, we will study a situation of four species with an absolute and a relative predator and two absolute preies without interaction among the latter ones. Here the cycle is derived and its period with the corresponding medium number are presented.

2.INTERACTION AMONG THREE SPECIES

Considering the Volterra analysis of interaction among three species, let x, y and z be the respective number of individuals in each of the three species. We assume a special case where the x and y represent the number of preies with unlimited resources and without compiting among themselves. The number of predators is z, and has as resource both preies. Thus, Volterra's differential equations for this system are.

$$\frac{dx}{dt} = (E_1 - c\, z)\, x$$
$$\frac{dy}{dt} = (E_2 - f\, z)\, y \qquad (1)$$
$$\frac{dz}{dt} = (-E_3 + m\, x + n\, y)\, z$$

Here the $E_i > 0$ are the values corresponding to the growth rate for each species. It is clear that because z represents the number of predators the sign of E_3 must be negative. On the other hand $c > 0$ and $f > 0$ measure the susceptibility to predation of species given by x and y. $m > 0$ and $n > 0$ measure the corresponding predator ability for feeding on the respective preies.

We now are going to show the existence of a cycle under certain general conditions.

From equation (1) turns out that

$$\frac{d}{dt}(f \ln x - c \ln y) = fE_1 - cE_2$$

and integrating this equations we obtain:

$$x^f y^{-c} = e^{k_1} e^{(fc_1 - cE_2)t} \quad (3)$$

where k_1 is the integration constant. Under the condition $fF_1 - cF_2 = 0$ we have

$$x^f y^{-c} = e^{k_1}$$

or

$$y = e^{-k_1/f} x^{F_2/F_1} \quad (4)$$

From here, we have that both preies have the same phase.
Now replacing the relation between y and x given by (4) in the third equation of (1), we obtain that

$$\frac{dx}{dt} = (F_1 - c\,2)\,x$$
$$\qquad (5)$$
$$\frac{dz}{dt} = (-E_3 + mx + n\,e^{-k_1/f} x^{E_2/F_1})\,z$$

On the other hand replacing x in term of y in equation (1) we have another system

$$\frac{dy}{dt} = (E_2 - fz)\,y \qquad (6)$$
$$\frac{dz}{dt} = (-F_3 + m\,e^{k_1/f} y^{E_1/E_3} + ny)\,z$$

These two systems given by (5) and (6) generalize Volterra's equations for two competitors. They have an adding term to an arbitrary power. It is clear that in the case $E_1 = E_2$ they both become Volterra's systems. (see [1] and [2]).
The next task is the solution of the system (5). Calling

$$p = n\,e^{-k_1/f}, \quad \alpha = p/E_3 (E_3/m)^{E_2/E_1}$$

and

$$X = \frac{m}{E_3} x, \quad Z = \frac{c}{E_1} z$$

therefore the system (5) it is reduced to

$$\frac{dX}{dt} = E_1 (1 - Z)\,X \qquad (7)$$
$$\frac{dZ}{dt} = E_3 (-1 + X + \alpha X^{E_2/E_1})\,Z$$

Now multiplying the new first equation by $E_3 \alpha X^{E_1/E_2}$ and the second one by E_1 and adding them up, we have

$$E_3 \alpha X^{E_1/E_2^{-1}} \frac{dX}{dt} + E_1 \frac{dZ}{dt} =$$

$$E_1 E_3 (\alpha X^{E_1/E_2} - Z + XZ) \qquad (8)$$

On the other hand multiplying the first equation of (7) by $-E_3$ and the second one by $E_1/2$, adding them up, it results

$$\frac{E_1}{Z} \frac{dZ}{dt} - E_3 \frac{dX}{dt} =$$

$$E_1 E_3 (-1 + \alpha X^{E_1/E_2} + XZ) \qquad (9)$$

From (8) and (9) it holds true that

$$\frac{d}{dt}(\ln Z^{E_1} - E_3 X - E_3 \alpha \frac{E_2}{E_1} X^{E_1/E_2} - E_1 Z) =$$

$$= E_1 E_3 (Z - 1) \qquad (10)$$

Now replacing $(Z - 1)$ from the first equation of (7), and integrating, we obtain

$$\zeta = Z^{E_1} e^{-E_1 Z} =$$
$$= \frac{1}{c} X^{-E_3} e^{E_3 X} +$$

where C in an integration constant. This equality determines two different functions of Z and X respectively which compared determine, in a similar fashion a Volterra did, the existence of a cycle in the phase spac (X,Z). Indeed, our first function is the same as in Volterra's analysis and the second, that is to say the function of X, is a perturbation of Volterra's corresponding one.
We note that the procedure to see the existence of the cycle in projection plane (Y, Z) using the system (6) is the same as one used for (X,Z).
The grapht of both functions ζ vs Z and ζ vs X are given in figure 1.

3. PERIOD COMPUTATION

Having the existence of the cycle, it is very interesting to try to compute the period of cycle near the equilibrium point.
From the first function defined by (11):

$$\zeta = \left(\frac{Z}{e^Z}\right)^{E_1}$$

derivating with respect to time, and after some intermediate operations we have:

$$dt = \frac{d\zeta}{E_1 E_3 \zeta (1-Z)(-1 + X + \alpha X^{E_1/E_2})} \qquad (12)$$

In order to compute the period, at this point we proceed as Volterra did, by decomposing the cycle into four parts which are determined by the four singular points. At these points the denominator of (12) is zero.

We remark that the second factor of the denominator has just one zero in the interval (0,1) for X. This is true for any E_1/E_2. Indeed, its root is a point satisfying

$$1 - X = \alpha X^{E_1/E_2}$$

which is in general a trascendental equation. Taking

$$Z = 1 + v_1$$

we obtain

$$1 - e\,\zeta^{1/E_1} =$$

$$v_1^2 \left(\frac{1}{2!} - \frac{1}{3!} + \frac{3 v_1}{4!} + \ldots\right) = v_1^2\, S(v_1)$$

from which

$$1 - Z = v_1 = \sqrt{1 - e\ \zeta^{1/\varepsilon_1}}\ \frac{1}{\sqrt{S(v_1)}} \quad (13)$$

On the other hand, making

$$X = 1 + v_2\ ,$$

then approximating only tothe second term, we have

$$X + \alpha X^{\varepsilon_1/\varepsilon_2} \simeq 1 + v_2 + \alpha + \alpha\varepsilon_1/\varepsilon_2\ v_2 + \alpha\ \varepsilon_1/\varepsilon_2(\varepsilon_1/\varepsilon_2 - 1)\ \frac{v_2^2}{2!} \quad (14)$$

which replaced in the formula (11) gives:

$$C\ \zeta^{-1/\varepsilon_3} = \frac{1 + v_2}{\exp[1 + v_2 + \varepsilon_2/\varepsilon_1{}^{\alpha}\ (1+v_2)^{\varepsilon_1/\varepsilon_2}]} \quad (15)$$

Now, developing $(1 + v_2)^{\varepsilon_1/\varepsilon_2}$ and taking into consideration only the two first terms, we have

$$1 - C\ e^{[1 + \varepsilon_2/\varepsilon_1{}^{\alpha}\ \ -1/\varepsilon_3]} =$$

$$1 - (1 + v_2)\ e^{-[(1+\alpha)v_2 + \alpha(\varepsilon_1/\varepsilon_2 - 1)\ \frac{v_2^2}{2!}]} \quad (16)$$

Developing the exponential convenien tly, the following expression is derived

$$1 - C\ e^{[1+\varepsilon_2/\varepsilon_1{}^{\alpha}\ \ \zeta\ -1/\varepsilon_3]} =$$

$$v_2(\alpha + \frac{v_2}{2}\ (1 + \alpha\ \varepsilon_1/\varepsilon_2 - \alpha - \alpha^2) + $$

$$+ v_2^2(-\frac{1}{3} - \frac{\alpha}{2} + \frac{\alpha^2}{2} - \frac{\alpha^2}{2}\varepsilon_1/\varepsilon_2 + \alpha^3/6)$$

$$= v_2\ p\ (v_2) \quad (17)$$

From here, it is possible to verify that then when $\alpha = 0$, then $p(v_2) = v_2\ S(v_2)$ thus turning out to be like Volterra's case. Replacing v_2 from (19) to (15) and deleting the second term having v_2^2 in $p\ (v_2)$ we obtain

$$-1 + X + \alpha X^{\varepsilon_1/\varepsilon_2} = \alpha +$$

$$+ \left[\frac{1 - C\ e^{1+\ \ 2/\ \ 1^{\alpha}}\ \zeta^{-1/\ \ 3}}{\alpha}\right].$$

$$[1 + \alpha^{\varepsilon_1/\varepsilon_2}] \quad (18)$$

Replacing this and (13) into (14) we obtain approximately

$$\frac{1}{4}\ T \simeq \frac{1}{\sqrt{2}\,\varepsilon_3}\ \int_{t_1}^{t_2} \left[\sqrt{t}(1-t)\ A - B\left(\frac{1-t}{e}\right)^{\varepsilon_1/\varepsilon_2}\right]^{-1} dt \quad (19)$$

where T is the period and it was used the change of variable: $t = 1\ e\ \zeta^{1/\varepsilon_1}$ have t_1 and t_2 correspond to the points ζ_1 and ζ_2 which represent the coordinate of two subsequent singular points

$$A = (\alpha + \varepsilon_1/\varepsilon_2 + 1/\alpha),$$

$$B = C\ e^{1+\alpha\varepsilon_2/\varepsilon_1}\ (1/\alpha + \varepsilon_1/\varepsilon_2)$$

with a further change of variables

$$x = \sqrt{t}$$

the integral in (22) becomes

$$\frac{1}{4}\ T \simeq -\frac{\sqrt{2}}{3} \int_{x_1}^{x_2} \frac{dx}{A(1-x^2) - B\ e^{\varepsilon_1/\varepsilon_2}(1 - x^2)^{1-\varepsilon_1/\varepsilon_3}}$$

This is a general expression and a good approximation of the period. We now are going to compute such an integral in a very particular case: $\varepsilon_1 = \varepsilon_3$. In such an instance we have

$$\frac{1}{4}\ T \simeq -\frac{\sqrt{2}}{3} \int_{x_1}^{x_2} \frac{d\ x}{A(1 - x^2) - B\ e}$$

$$-\frac{\sqrt{2}}{3}\ \frac{2}{[-4A(A-Be)]^{1/2}}\ \text{arc tg}\left[\frac{-2\ Ax}{4(-A)\ (A - Be)^{1/2}}\right]_{x_1}^{x_2} \quad (21)$$

4. MEDIUM VALUES

Having computed the period, it is important to consider some relations with medium values of the number of species in the competitive system. For this, consider the first equation of (7) from which

$$\frac{d}{dt} \log X = \varepsilon_1\ (1 - Z)$$

is derived. Integrating between two times t_1 and t_2, in which X_1 and Z_1 assume:

$$\log \frac{X_2}{X_1} = \varepsilon_1(t_2 - t_1) - \varepsilon_1 \int_{t_1}^{t_2} Z\ dt$$

By extending the range of integration to one period, T, the left side goes to zero, and

$$\frac{\varepsilon_1}{C} = \frac{1}{T} \int_0^T Z\ dt \quad (22)$$

On the other hand, by considering the third equation of (1) we get similarly

$$\varepsilon_3 = \frac{1}{T}\left[\ m\int_0^T x\ dt + n\int_0^T y\ \ dt\right] \quad (23)$$

5. FOUR SPECIES COMPETITION

In the previous sections we have seen considerations of three species competition. We are going to extend our study to cases which include four competing species. To give some light to the general cases, we will derive. as consequences, some interesting facts about three competing species when one special species has no individuals at the initial time.

Consider the competition among two species, a relative predator and an absolute predator. Let x, y be the number of the first two kind of preies. Let z be the number of the relative prey and predator and finally w the number of the absolute

predator.
The relative prey and predator feed on the first two preies and it is prey of the absolute predator. Thus, the differential equations for this system are:

$$\frac{dx}{dt} = (\varepsilon_1 - a z)\, x$$

$$\frac{dy}{dt} = (\varepsilon_2 - b z)\, y$$

$$\frac{dz}{dt} = (-\varepsilon_3 + cx + ey - fu)\, z \tag{24}$$

$$\frac{d\omega}{dt} = (-\varepsilon_4 + g z)\, \omega$$

we wish to fird a cycle. In order to do this, from the first two equations we derive

$$\frac{x^b}{y^a} = e^{(\varepsilon_1 b - \varepsilon_2 a)\, t}\, \bar{e}^{c_1}$$

where c_1 is an integrating constant.
With the condition $\varepsilon_1 b - \varepsilon_2 a = 0$

$$x = y^{\gamma_1}\, e^{c_1 \gamma_1 / a} \tag{25}$$

where $\gamma_1 = \varepsilon_1 / \varepsilon_2$
In a similar way from the second and fourth equations, it is possible to derive

$$\omega = y^{-\gamma_2}\, e^{c_2 \gamma_2 / g} \tag{26}$$

where $\gamma_2 = \varepsilon_4 / \varepsilon_2$ and C_2 an integrating constant.
Replacing (25) and (26) in the third equation of (24) and calling.

$$\alpha\ \frac{c}{\varepsilon_3} \left(\frac{\varepsilon_3}{e}\right)^{1} e^{c_1/a\ \gamma_1}\ ;$$

$$\beta = \left(\frac{f}{\varepsilon_3}\right)\left(\frac{\varepsilon_3}{e}\right)^{\gamma_2} e^{c_2/g\ \gamma_2}$$

and

$$Y = \frac{e}{\varepsilon_3}\, y\ , \qquad Z = \frac{b}{\varepsilon_3}\, z$$

the second and third equation of (24) become

$$\frac{dY}{dt} = \varepsilon_2\, (1 - Z)\, Y$$

$$\frac{dZ}{dt} = -\varepsilon_3\, (1 - Y - \alpha Y^{\gamma_1} + \beta Y^{-\gamma_2}) Z$$

Now well will derive the cycle in the (Y, Z) plane. Multiplying the first equation of (27) by $\varepsilon_3 (\alpha Y^{\gamma_1 - 1} - \beta Y^{-\gamma_2 - 1})$ and the second one by ε_2 and adding:

$$\varepsilon_3 (\alpha Y^{\alpha_1 - 1} - \beta Y^{-\gamma_2 - 1}) \frac{dY}{dt} +$$

$$\varepsilon_3 \frac{dZ}{dt} = \varepsilon_2 \varepsilon_3 (\alpha Y^{\gamma_1} - \beta Y^{\gamma_2} - Z + ZY) \tag{28}$$

Now multiplying the first of (27) by $-\varepsilon_3$ and the second by $\frac{\varepsilon_2}{Z}$ and adding, we have

$$\frac{\varepsilon_2}{Z} \frac{dZ}{dt} - \varepsilon_3 \frac{dY}{dt} = \varepsilon_2 \varepsilon_3$$

$$(-1 + \alpha Y^{\gamma_1} + \beta Y^{-\gamma_2} + ZY) \tag{29}$$

Equalizing (28) and (29) and replacing $\varepsilon_1 \varepsilon_3 (1 - Z)$ by using the first equation of (27) and integrating, it holds true

$$\zeta = \left(\frac{Z}{e^Z}\right)^{\varepsilon_2} = \frac{1}{C}\left[\frac{Y}{e^{\alpha/\gamma_1 Y^{\gamma_1} + \beta/\gamma_2 Y^{\gamma_2} + Y}}\right]^{-\varepsilon_3}$$

Both functions derived by this integral are of the same shape as those in the previous case with three competing species.
From here we have the existence of the cycle in the space(Y,Z) and therefore by the relations with the other variables, the existence of the cycle in the space (x,y,z,μ).
It is worth noting that if the pertubation in the second equation is given in a more general way by a polynomial or even more by an analytic function, the existence of the cycle might be derived similarly as we did here.

6. PERIOD COMPUTATION FOR FOUR SPECIES

Having obtained the existence of the cycle, it is important to know about the period of the cycle around the equilibrium point. The general analysis is analogous to what we have developed in Section 3 with a slight difference. For this reason we include the main facts.
Taking the derivate of (33) we have

$$dt = \frac{d\zeta}{\varepsilon_1 \varepsilon_2 \zeta\, (1-Z)\, (-1 + Y + \alpha Y^{\gamma_1} \beta Y^{-\gamma_2})} \tag{31}$$

and again with

$$Z = 1 + v_1$$

the equation to be derived is the same as (14). On the other hand with

$$Y = 1 + v_2$$

it turns out

$$-1 + Y + \alpha Y^{\gamma_1} - \beta Y^{-\gamma_2} = (\alpha - \beta) + v_2$$

$$\{(1 + \gamma_1 \alpha + \beta \gamma_2) + [\alpha \gamma_1 (\gamma_1 - 1) - \beta \gamma_2 (\gamma_2 - 1)] \frac{v_2}{2!}\} \tag{32}$$

At last we arrive to

$$1-e^{1+a+b}C\,\xi^{-1/\varepsilon_3} =$$

$$= v_2\left[(a\gamma_1 - b\gamma_2) \pm \frac{v_2}{2!} \right. \qquad (33)$$

$$\left. (a\gamma_1 + 1 - b\gamma_2)\right] = v_2\, p\,(v_2)$$

where

$a = \alpha/\gamma_1$ and $b = \beta/\gamma_2$

We note that similarly to the case of three species, when $\alpha = \beta = 0$, $p(v_2)$ equals $S(v_2)$ as in Volterra's case. Replacing (33) in (32) and this in (31), after some considerations it holds true

$$\frac{1}{4}\,T \simeq \frac{1}{\sqrt{2\varepsilon_2\varepsilon_1}}$$

$$\int_{\xi_1}^{\xi_2} \frac{d}{\xi\sqrt{1 - e\xi^{1/\varepsilon_2}}\left[p + D\,\xi^{-1/\varepsilon_3}\right]} \qquad (34)$$

where

$$p = C\,e^{1+a+b} + \frac{\gamma_1\alpha}{\alpha-\beta} + \frac{\beta\gamma_2}{\alpha-\beta}$$

and

$$D = \frac{k\,e^{1+a+b} - \alpha\gamma_1 - \beta\gamma_2}{\alpha - \beta}$$

It is worth noting that the integral in (34) coincides with the integral given in (19). Therefore tha same (21) holds for the periods in this case, with suitable new constants and new limits.

The medium values are obtained in a similar way as in the case of three species. Therefore we do not include them.

7. AN EXAMPLE

In this section we are going to consider two interesting example of the case of three and four competing species. In the first example, we consider the case where the parameters are :

$\varepsilon_1 = 2$; $\varepsilon_1 = 1$; $\varepsilon_3 = 2$; $c = 1$; $f = .5$, $= 1$ and $= .5$

with an initial point

$X(0) = 2$, $y(0) = 1$ and $Z(0) = .2$

With these values, we have the graphic 2. Moreover in Fig. 2 we have the cycle in the plase space.

In the second example, we consider the case where the parameters values are:

$\varepsilon_1 = 2$; $\varepsilon_1 = 1$; $\varepsilon_3 = 2$; $_4 = 2$; $a = 1$, $b = .5$, $c = 1$; $g = 1$

with the initial condition

$x(0) = 1$, $y(0) = 2$; $z(0) = .2$ and $w(0) = .5$

We present en Fig. 3 the number of individuals as function of time

Bibliography

(1): Volterra, A: Variazioni e fluttuazioni del numero d'individui is specie animali conviventi. R. Comitato Talassografico Italiano, Memoria 131:1-142.1927

(2) Scudo, F.M. and J.R. Ziegler: The golden age of theoretical ecology 1923-1940. Lectnre Notes in Biomathematics N°22 Springer 1978

(3) Goel. N.S., S.C. Maitra and F.W. Montroll: On the Volterra and and other nonlinear models of interacting population. Rev. Mod. Phys. Vol. 42 N°s. Part 1 231-276 1971

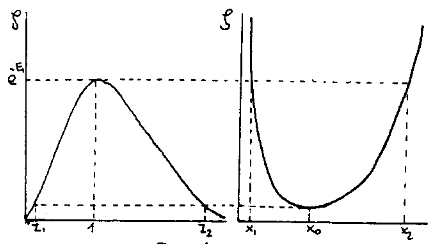

Fig 1

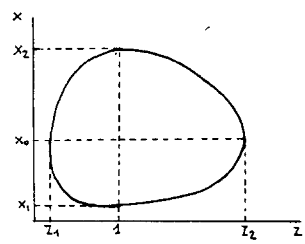

Fig 2

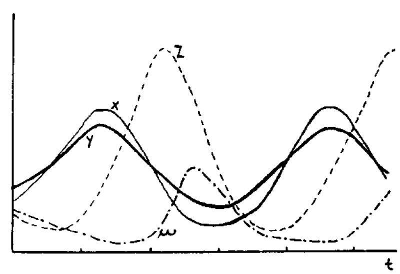

Fig. 3